# GIANT SEQUOIA (*SEQUOIADENDRON GIGANTEUM* [TAXODIACEAE]) SEEDLING SURVIVAL AND GROWTH IN THE FIRST FOUR DECADES FOLLOWING MANAGED FIRES

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## Abstract

Giant sequoia (*Sequoiadendron giganteum*) seedling survival was nearly seven (6.78) times greater in heavily charred soils than in non-burned soils 34 and 35 yr after the first experimental burns in Kings Canyon National Park, California, and the first such management burns in any western national park. Tree height, especially trees growing in intensely burned areas, was found to be highly correlated with sunlight and less so with moisture. Moisture and light were important to establishment of giant sequoias but continued growth of these trees in the first four decades of life appears to be more dependent on high levels of sunlight. Surveyed vegetation and downed wood indicated that 35 yr after management burns stand structure has developed to the point where the management areas are susceptible to destructive crown fires.

Key Words: Giant sequoias, Sequoiadendron giganteum, seedlings, survivorship, fire.

Fire is necessary for giant sequoia (Sequiadendron giganteum [Lindl] Buchh.) reproduction. It removes surface litter and duff and opens up the forest canopy (Kilgore and Biswell 1971) thereby creating the conditions necessary for seedling germination and growth of what (Stephenson 1994) described as a "pioneer species" (one that requires a "canopy-destroying disturbance to complete its life cycle"). Conversely, it is known that few to no giant sequoia seedlings become established in the thick duff of infrequently burned groves (Kilgore and Biswell 1971; Hartesveldt and Harvey 1967; Hartesveldt et al. 1975; Harvey et al. 1980). While the intensity and duration of fire necessary to promote effective reproduction is still a matter of controversy (Stephenson et al. 1991; Stephenson 1996), it is known that hot fires burning in dense stands of mature giant sequoias produce as many as 100,000 seedlings per hectare following heatinduced seed fall (Hartesveldt et al. 1975). Hot fires, however, also threaten groves if they have a "fire-ladder" type of vegetation that allows fire to spread into the canopy (Parsons and Botti 1996; Stephenson 1994).

The present study reports on the growth of young giant sequoias and factors affecting their survival following experimental fires set in 1965 and 1966 in Redwood Canyon, Kings Canyon National Park. At the time they were set, these fires were the first experimental burns in a coniferous forest ecosystem in a western national park. The associated Hartesveldt Study (Hartesveldt et al. 1975; Harvey et al. 1980) and subsequent research (Harvey and Shellhammer 1991) is a rare long-term study in which over 7000 seedlings established after the original management fires were individually identified and have been monitored since. The objective of the present work was to identify key factors affecting their growth during the 35 yr following the controlled burns. We also report on the build up of duff, litter, downed wood, and of the subcanopy of trees and bushes between the time of the burns in 1965 and 1966 and this study in 2000.

#### **METHODS**

Four study areas were established as controlled burn sites in the Redwood Mountain Grove of Kings Canyon National Park, California, in 1964–66. Giant sequoia seedlings did not survive past five years post-burn in two of the areas, Ridge and North, due primarily to shading by dense tree cover in Ridge Area or dense ground cover (primarily *Lupinus* spp.) in North Area (Harvey et al. 1980) but individuals persisted to 2000 in the other two areas, i.e., Trail, burned in 1965, and South, burned in 1966 (Figs. 1 and 2). The manipulated portions of these two areas are approximately 1.8 hectares each and both have a base elevation of 1611 m (5540 ft.). Trail Area

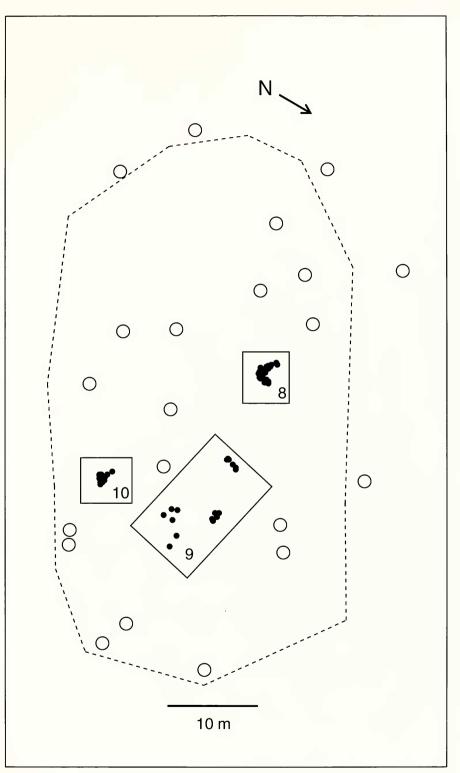


FIG. 1. Map of Trail area including large, established Giant Sequoia (O), seedlings from control burn (•) and burn area boundary (dashed line). Subareas are identified as numbered rectangles but do not represent the physical boundaries for each subarea.

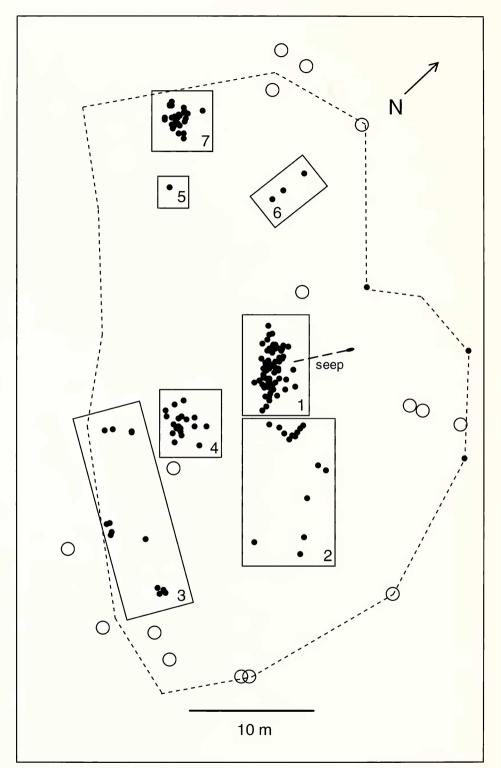


FIG. 2. Map of South area including large, established Giant Sequoia ( $\bigcirc$ ), seedlings from control burn ( $\bullet$ ) and burn area boundary (dashed line). Subareas are identified as numbered rectangles but do not represent the physical boundaries for each subarea.

Area	Subarea	Treatment	No. of seedlings	Density	Moisture rank	Light rank	Proximity to big trees
South	1	burn pile	69	dense	1	7	far
South	2	mixed	15	scattered	3	5	far
South	3	non-burn pile	13	scattered	4	6	mixed
South	4	burn pile	19	mixed	5	4	close
South	5	burn pile	1	1 tree	7	1	far
South	6	burn pile	3	3 trees	9	3	far
South	7	non-burn pile	36	dense	2	8	far
Trail	8	burned	42	dense	8	9	far
Trail	9	mixed	17	scattered	6	2	far
Trail	10	mixed	18	scattered	10	10	mixed

TABLE 1. CHARACTERISTICS OF SUBAREAS WITHIN SOUTH AND TRAIL AREAS. Rankings for average moisture and average light are from highest (1) to lowest (10) 10% subdivisions. Proximity to nearest mature giant sequoias; Far  $\geq 8$  m, Close  $\leq 4$  m, and Mixed = trees scattered at various distances to nearest large trees.

faces east, has a  $17^{\circ}$  degree slope and is moderately rocky. South Area faces west and is generally level with  $10^{\circ}$  degree or less slopes on one quarter of the site. It has few rocks in its soil. The soil in both areas is a gray-brown podzolic type with a texture varying between fine sand and sandy loam (Harvey et al. 1980).

The two areas had heavy accumulations of downed fuel in the 1960s hence logs and felled snags were cut into sections, piled and burned (producing a burn pile substrate) in Trail Area in 1965 and in South Area in 1966; temperatures beneath the burn piles reached 600° F from 2.5 to 7.5 cm below the surface of the soil (Hartesveldt and Harvey 1967). Bare mineral soil (i.e., scarified substrate) was exposed in some portions of the two areas by the heavy equipment used to move the logs. Other surfaces (i.e., burned substrate) within the areas supported enough fuel to carry surface fires and a few areas supported a mix of scarified and burned substrates.

A total of 7015 seedlings were identified and tagged in Trail and South Areas and monitored at various times over the last four decades (Harvey et al. 1980; Harvey and Shellhammer 1991). These individuals (many now sizable trees) were located in mid-July 2000, measured for height and their precise locations mapped using ultrasonic distance finders (SONIN Combo Pro, SONIN Inc., White Plains, NY) and a triangulation technique (Quigley and Slater 1994). Soil moisture readings as measures of capacitance were taken at 65 to 75 cm depths and from 30 to 60 cm from the base of each individual using a Model 200 Aquaterr Moisture Meter during the middle of summer on July 17th and 18th, 2000. The readings in percent soil moisture were taken in each area on consecutive days to gain an idea of the relative differences in soil moisture between trees and areas during the middle of the summer. Light levels were measured using a Li-Cor 250 light meter. Measurements were taken at the top of smaller individuals and at 2 m above ground level on taller individual trees. Light measurements were performed eight times on one day (hourly between 9 a.m. and 4 p.m.) for each area, the two areas being monitored on consecutive days (July 23rd and 24th) when skies were cloudless. Light intensity readings (in  $\mu$ mols s<sup>-1</sup> m<sup>-2</sup>) were summed over the 8-hour period and used to compare the relative differences in light between trees and areas. Finally, three line transects were run across each area between randomly selected mature giant sequoias at the edges of the treatment areas; South Area was monitored on July 18th and Trail on July 28th, 2000. Plant species or wood and bark were identified and measured for height or other parameters at onemeter intervals. Mature giant sequoias (with a diameter at breast height (dbh)  $\geq 2$  m) within the areas have long been identified and were located as part of the seedling survey, as were intermediate size giant sequoias (less than 0.3 m dbh) that existed before the experimental burns. No giant sequoias with dbh less the 2 m and more than 0.3 m were present. Coniferous trees of other species were either shrub level trees of 4 m or less in height or larger trees with dbh of 0.3 m or greater and heights of greater than 33 m. The former, shorter trees were included in the line transects while the latter, taller trees were counted but not individually located by survey.

Because their numbers were so small, we combined the individuals derived from all treatments other than "burn pile" (i.e., scarified substrates, burned substrates, and mixed scarified and burned substrates) and categorized them as being "non-burn pile" substrates. Individuals in South and Trail Areas were grouped into "subareas", numbered 1 through 10, based not on physical boundaries but on their pattern of distribution, amount of shade, and treatment, i.e., burn pile or non-burn pile (Table 1, Figs. 1) and 2). Trail Area, for example, was divided into three subareas, two of which had tightly-clumped burn-pile individuals (Subarea 10 was heavily shaded by an over-story of bushes and Subarea 8 was low in moisture and had moderate light)

		Height (cm)		Moisture (%)		Light ( $\mu$ mols s <sup>-1</sup> m <sup>-2</sup> )	
Area	Ν	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Trail	77	208ª	186	26 <sup>a</sup>	12	3369 <sup>a</sup>	2467
South	156	356 <sup>b</sup>	228	52 <sup>b</sup>	15	3741ª	1988

TABLE 2. DESCRIPTIVE STATISTICS OF TRAIL AND SOUTH AREAS. Means with the same superscript are not significantly different at  $\alpha = 0.05$ . Light measurements are based on the total of eight measurements taken in one day.

while the third subarea (Subarea 9) included the rest of the trees, mostly non-burn pile individuals in Trail Area which were more widely distributed in more open conditions. Subarea and burn pile versus non-burn pile designations for each individual facilitated comparisons within and between treatment areas and among subareas. Subareas 6 (three survivors) and 7 were excluded from further analysis due to undetermined effects of a management fire that burned into those subareas (circa 1985) as well as the one tree that made up Subarea 5 (because of its small sample size); those exclusions reduced the total number of trees used in the analysis by 17% (40 of 233 individuals).

Descriptive statistics were performed on measured variables (height, moisture, and light) for trees within areas and subareas using Excel software (Microsoft 2002). Analysis of variance, examining area, subarea, and burnpile effects on tree height, was performed using SAS software (2001). In instances where significant treatment effects occurred, a Tukey's Studentized Range test ( $\alpha = 0.05$ ) was used to compare the differences among these treatments. Correlations and multiple linear regressions were performed on measured variables using SAS software. Soil surface treatment categorical data was assigned a value of 1 for burn pile and 0 for non-burn pile. Correlations and regressions were run twice, once when analyzing subareas 1 through 4 and 8 through 10 (Table 4a) and then also excluding Subarea 1 (Table 4b). We chose to remove Subarea 1 for part of our analyses because it was much moister than the soil moisture conditions common to most giant sequoia groves and hence we did not think it was representative.

### RESULTS

The survival success for seedlings in burn piles in South Area (from 1967 through 2000) was 26% (80 of 312) vs. 3% for non-burn pile treatments (51 of 1561); in Trail Area, the survival percentage was 13% (50 of 377) vs. 0% (24 of 4765) for burn pile and non-burn pile treatments. When South and Trail are combined the average survival percentages for burn pile seedlings is 19% as compared with 1% for non-burn pile seedlings, hence giant sequoia seedlings that grew and survived from 1966–67 to 2000 in burn pile substrates had nearly seven times greater survival percentage than those on all other substrates.

South Area was significantly moister than Trail (average soil moisture of 52% vs. 26%, p < 0.05) and had the most overall sunlight (3741 vs. 3369 µmols s<sup>-1</sup> m<sup>-2</sup>) based on midsummer measurements (Table 2). The average height of seedlings in South was significantly greater than those in Trail (356 cm vs. 208 cm, p < 0.05, n = 231, t-test). The average height of the 10 tallest trees in both areas (8 in South and 2 in Trail) was 876 cm; they had an average growth rate of 25 cm per year. In contrast the ten shortest trees in the two areas averaged 51.6 cm in height and had an average growth rate of approximately 1.47 cm per year.

When examining differences among subareas it is important to note that the midsummer soil moisture in Subarea 1 (the large group of trees growing near a seep in South Area) was significantly greater than and Subarea 10 (the suppressed group of very short individuals in Trail Area) was significantly lower than all other subareas (p < 0.05, n = 7, Tukey's Studentized Range test) while midsummer light levels of various subareas were not significantly different from one another due to the large sunlight variance within each subarea (Table 3). Trees in subareas 1 (near a seep), 4 and 9 (in strong sun) were significantly taller (p < 0.05, n = 7, Tukey's Studentized Range test) than the trees in the other subareas. Subarea 1 had the highest average midsummer soil moisture while Subarea 9 had the highest average midsummer light.

Initial multiple regression analysis indicated that light and surface treatment were highly significant to tree height. This analysis also indicated a significant moisture  $\times$  surface treatment interaction. Reanalysis within each surface treatment category (burnpile verus non-burnpile) reaffirmed the importance of light and revealed the interplay between moisture and light. When including Subarea 1 (the area with the significantly highest moisture) in the analyses, light and moisture are individually important for trees in burnpile treatments (Table 4a). This result was affected greatly by the large numbers of trees in the wet, burnpile group identified as Subarea 1. The analysis of all non-burnpile trees revealed significant effects of both moisture and a moisture  $\times$  light interaction on tree height. When trees were analyzed without those in Subarea 1

		Height (cm)		Moisture (%)		Light ( $\mu$ mols s <sup>-1</sup> m <sup>-2</sup> )	
Subarea	N _	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
1	69	463 <sup>a,b,c</sup>	240	63ª	11	3329 <sup>b,c,d,e,f,g,h</sup>	1934
2	15	$173^{c,d,e,f,g}$	118	$45^{b,c,d,e,f}$	11	$4553^{a,b,c,d,e,f,g}$	2038
3	13	$138^{d,e,f,g,h}$	66	39 <sup>b,c,d,e,f</sup>	6	4119 <sup>a,b,c,d,e,f,g,h</sup>	2423
4	19	341 <sup>a,b,c,d,e</sup>	200	$38^{c,d,e,f}$	8	4874 <sup>a,b,c,d,e,f</sup>	1544
7	36	314 <sup>b,c,d,e</sup>	162	$48^{b,c,d}$	12	$3211^{b,c,d,e,f,g,h}$	1657
8	42	149 <sup>e,f,g,h</sup>	94	$28^{f,g}$	11	2921 <sup>c,d,e,f,g,h</sup>	2320
9	17	438 <sup>a,b,c,d</sup>	261	35 <sup>c,d,e,f,g</sup>	11	5787 <sup>a,b,c,d</sup>	2223
10	18	127 <sup>e,f,g,h</sup>	40	12 <sup>h</sup>	3	2132 <sup>d,e,f,g,h</sup>	1268

TABLE 3. MEANS COMPARISONS AMONG SUBAREAS. Means with the same superscript are not significantly different from each other at  $\alpha = 0.05$ .

(Table 4b) light was the single determinant of tree height in the burnpiles. In both analyses, none of the selected variables were highly correlated with each other (r < 0.85).

Both Trail and South Areas have become crowded with surface litter, plants and an extensive subcanopy of shrubs and small trees (Table 5). Almost 50% of South is covered with shrubs and small trees averaging 2.1 m in height while Trail has 49% cover averaging 3.2 m. Fifteen and 12% respectively of the surfaces of South and Trail are covered by downed wood and bark.

#### DISCUSSION

The value of heavily burned soil to giant sequoia seedling survival has increased with time (Hartesveldt et al. 1975; Harvey et al. 1980;

 $8.6 \times 10^{-4}$ 

Moisture  $\times$  light

Harvey and Shellhammer 1991, and present paper for studies in 2000). The proportion of individuals surviving in burn piles compared to those surviving in all of the treatments has grown from 2.5 to 3.5 times greater in 1990 (Harvey and Shellhammer 1991) to nearly 7 times (6.78 times) greater in 2000. Heated soils in giant sequoia groves can be more wettable and friable after intense heating (Donaghey 1969) and it is likely that heating kills seeds of competing species and pathogens in the soil (Harvey and Shellhammer 1991). Those benefits appear to continue in to the first few decades of the seedlings' lives as burn pile individuals were significantly taller than nonburn pile individuals (p < 0.05) after 34 to 35 yr, particularly those with higher soil moisture and/ or light.

Trail Area had more initial seedlings (5142 versus 1873 for South Area) but had a poorer

2.06

0.046

TABLE 4. MULTIPLE LINEAR REGRESSION PARAMETERS PREDICTING SEEDLING HEIGHT.

Across all burnpile trees           Intercept $3.785$ $0.204$ $18.53$ $<0.001$ Light $0.020$ $0.006$ $3.34$ $0.001$ Moisture $0.026$ $0.004$ $6.22$ $<0.001$ Moisture × light $-9.3 \times 10^{-5}$ $1.2 \times 10^{-4}$ $-0.78$ $0.438$ Across all non-burnpile trees           Intercept $5.045$ $0.420$ $12.33$ $<0.001$ Light $-0.004$ $0.014$ $-0.31$ $0.759$ Moisture $-0.034$ $0.013$ $-2.48$ $0.018$ Moisture × light $8.6 \times 10^{-4}$ $4.1 \times 10^{-4}$ $2.06$ $0.046$ 4b. Analysis of subareas 2-4. 8-10 (excluding Subarea 1)         Variable         Significance           Variable         Estimate         Standard Error         t value         Significance           Intercept $4.155$ $0.274$ $15.13$ $<0.001$ Variable         Estimate         Standard Error         t value         Significance           Moisture					
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Moisture × light $8.6 \times 10^{-4}$ $4.1 \times 10^{-4}$ $2.06$ $0.046$ 4b. Analysis of subareas 2–4, 8–10 (excluding Subarea 1)         Variable         Estimate         Standard Error         t value         Significance           Variable         Estimate         Standard Error         t value         Significance           Intercept         4.155 $0.274$ 15.13         <0.001           Light         0.019         0.007         2.71         0.008           Moisture         0.007 $0.009$ $0.73$ 0.468           Moisture × light $4.0 \times 10^{-5}$ $2.0 \times 10^{-4}$ $0.20$ 0.839           More response         Across all non-burnpile trees           Intercept $5.045$ $0.420$ $12.33$ $<0.001$ Light $-0.004$ $0.014$ $-0.31$ $0.759$	Light	-0.004	0.014	-0.31	0.759
2         4b. Analysis of subareas 2–4, 8–10 (excluding Subarea 1)         Variable       Estimate       Standard Error       t value       Significance         Across all burnpile trees       Intercept       4.155       0.274       15.13       <0.001         Light       0.019       0.007       2.71       0.008         Moisture       0.007       0.009       0.73       0.468         Moisture × light       4.0× 10 <sup>-5</sup> 2.0× 10 <sup>-4</sup> 0.20       0.839         Across all non-burnpile trees         Intercept       5.045       0.420       12.33       <0.001         Light       -0.004       0.014       -0.31       0.759	Moisture	-0.034	0.013	-2.48	0.018
Variable         Estimate         Standard Error         t value         Significance           Across all burnpile trees           Intercept         4.155         0.274         15.13         <0.001	Moisture $ imes$ light	$8.6  imes 10^{-4}$	$4.1 \times 10^{-4}$	2.06	0.046
Across all burnpile trees           Intercept         4.155         0.274         15.13         <0.001           Light         0.019         0.007         2.71         0.008           Moisture         0.007         0.009         0.73         0.468           Moisture × light $4.0 \times 10^{-5}$ $2.0 \times 10^{-4}$ 0.20         0.839           Across all non-burnpile trees           Intercept         5.045         0.420         12.33         <0.001           Light         -0.004         0.014         -0.31         0.759	4b. Analysis of subare	eas 2-4, 8-10 (excludin	g Subarea 1)		
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Variable	Estimate	Standard Error	t value	Significance
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Moisture $0.007$ $0.009$ $0.73$ $0.468$ Moisture × light $4.0 \times 10^{-5}$ $2.0 \times 10^{-4}$ $0.20$ $0.839$ Across all non-burnpile treesIntercept $5.045$ $0.420$ $12.33$ $<0.001$ Light $-0.004$ $0.014$ $-0.31$ $0.759$	Intercept	4.155	0.274	15.13	< 0.001
Moisture × light $4.0 \times 10^{-5}$ $2.0 \times 10^{-4}$ $0.20$ $0.839$ Across all non-burnpile treesIntercept $5.045$ $0.420$ $12.33$ $<0.001$ Light $-0.004$ $0.014$ $-0.31$ $0.759$	Light	0.019	0.007	2.71	0.008
Across all non-burnpile trees           Intercept         5.045         0.420         12.33         <0.001           Light         -0.004         0.014         -0.31         0.759	Moisture	0.007	0.009	0.73	0.468
Intercept         5.045         0.420         12.33         <0.001           Light         -0.004         0.014         -0.31         0.759	Moisture $\times$ light	$4.0 \times 10^{-5}$	$2.0  imes 10^{-4}$	0.20	0.839
Light -0.004 0.014 -0.31 0.759		Α	cross all non-burnpile tree	s	
	Intercept	5.045	0.420	12.33	< 0.001
Moisture $-0.034$ $0.013$ $-2.48$ $0.018$	Light	-0.004	0.014	-0.31	0.759
	Moisture	-0.034	0.013	-2.48	0.018

 $4.1 \times 10^{-4}$ 

#### MADROÑO

5.a Ground cover					
South Area % cover		Species	Trail Area	% cover	
36.53	litter,	duff	41.64 4.49		
20.33	Rubus	spp.			
16.10	downe	ed wood/bark	11.	87	
8.49	Lupini	us latifolius	13.	08	
4.90	Castill	leja disticha	<1.	00	
3.50		nia uniflora	5.67		
0.00	Galiun	n sparsiflorum	3.	15	
2.61		californica	2.15		
0.00	Rock		2.60		
0.00	Castill	leja spp.	2.	15	
1.99		caulon bicolor	6.	80	
1.78	Potent	tilla glandulosa	<1.	00	
1.10	Dispor	um trachyandrum	1.	82	
1.01		cium albiflorum	<1.	00	
<1.66		er species	<1.	58	
5.b Downed wood/bark					
South Area % cover		Condition	Trail Area %	6 cover	
1.99	Sound, <0.6 m		1.33		
2.26	Se	ound, >0.6 m	0.39		
1.42	R	otten, $<0.6$ m	4.49		
8.69	R	otten, $>0.6$ m	3.80		
0.74	Bark		1.90		
5.c Shrub/small tree subc	anopy				
South Area % cover	Height (m)	Species	Trail Area % cover	Height (m)	
15.46	0.9	Ceanothus parvifolius	2.08	3.0	
12.58	3.9	Abies concolor	15.03	3.6	
10.09	0.9	ferns	0.00	0.0	
7.84	3.1	Ceanothus integerrimus	8.13	4.4	
1.55	4.4	Cornus nuttallii	14.59	2.1	
1.28	0.9	Ribes cereum	0.74	1.2	
0.95	0.6	Ribes roezlii	0.54	1.4	
0.00	0.0	Calocedrus decurrens	6.26	2.6	
0.00	0.0	Pinus lambertiana	0.62	7.6	
0.00	0.0	Sequoiadendron	0.08	1.1	
Total	Average		Total	Average	
49.75%	2.1		48.75%	3.2	

TABLE 5. GROUND, SHRUB AND SMALL TREE COVER BY AREA. Nomenclature follows Hickman (1993).

survival rate for both burn pile and non-burn pile seedlings, primarily because of significantly less soil moisture in burn pile areas (i.e., Subareas 8 and 10) and less moisture and heavy overtopping by shrubs and small trees (Subarea 8); these two subareas, that had the shortest individuals, had the least soil moisture and the least light of any of the 10 subareas (Table 3).

Assuming it is reasonable to extrapolate from the mid-summer moisture and light measurements to longer periods of time, it appears that the moisture-light interaction is likely to be more important in the early years of growth (i.e., without enough soil moisture or light seedlings die) and that light generally becomes more important after that except in areas of high soil moisture, such as Subarea 1 in South where the tallest trees are growing in slightly below average light. After desiccation and insect damage killed most seedlings in both areas in their first and second years (Harvey et al. 1980) many of the individuals that survived have grown well in conditions ranging from relatively low moisture and high light (as in Subarea 9) to high moisture and relatively low light (as in Subarea 1). When both moisture and light are low, as in Subarea 8 in Trail Area, height has been greatly reduced. The seedlings that have generally grown the tallest, however, were trees (in Subarea 9 in Trail Area) growing more or less equidistant from mature trees where we assume they have experienced less root competition and have received relatively high amounts of light. In this context, our results agree in part with those of (Demetry 1995) who found that the taller seedlings, and later young trees, were at gap centers where there was less root competition. She found that the height of seedling in gaps was associated with water availability whereas we found that the tall individuals living in naturally-occurring gaps (e.g., those in Subarea 9) were experiencing high light levels and only moderate moisture compared to other trees in this study. Light is very important when seedlings are found in crowded conditions, as were found in the moist Subarea 1. Less light is partially compensated for by high moisture is very moist areas but high light is necessary for continued growth as we found some of our tallest trees in areas of high light and modest to low moisture. The impact of the burnpile treatment is clearly evident in the number and vigor of the survivors. For this treatment, light is the key player in determining tree height. In the non-burnpile treatments, the interaction of light with moisture is important. For the smallest trees in these treatments, light is the limiting agent irregardless of moisture. On the other hand, the tallest trees have high light and at least modest moisture.

The fact that the tallest trees in our study are growing in areas relatively far from mature giant sequoias is partially the result of the burn pile placement. Burn piles were interspaced between mature trees so as not to heat kill or damage the big trees; the 1965 and 1966 burns, after all, were the first experimental use of fire in a western national park and it appears in retrospect that we were overly careful to avoid heat damage to the mature sequoias. Five of the tallest individuals, however, (including the 4th and 7th tallest) are non-burn pile trees in Subarea 9 in Trail Area. These trees are growing in high light and moderate to low moisture conditions are usually equidistant and relatively far away from the nearest mature giant sequoias. In this general area, desiccation and later root competition from the big trees is likely to have killed off the hundreds of seedlings that originally germinated between them and the nearest big trees. The tree we identify as being the only individual in Subarea 5 (Table 3, Fig. 2) was the 8th tallest tree in the study and was growing in an area of very high light and low soil moisture and was located away from mature giant sequoias. In contrast, individuals in Subarea 8 (in Trail Area) are a few meters from a small seep arising between several big trees upslope of them but they did not benefit from it. They are within the root zone of the nearest giant sequoia and that may partially account for the low soil moisture in that subarea. The low moisture plus their density and associated competition appears to account for their low average height. It seems apparent to us that while soil moisture and light are necessary for germination and establishment, recruitment (i.e., individuals that have grown into trees of reproductive age) is more dependent on abundant light and to some degree distance from preexisting mature trees than soil moisture alone.

The assignment of subareas was based on soil surface treatment at the time of the burn (1965 & 1966) in addition to the resultant pattern of tree distribution (2000). In this manner, true replication of subarea conditions was not possible. Pseudoreplication issues such as this, while acknowledged by the authors (Hurlbert 1984) as common to fire ecology research, do not preclude us from drawing conclusions about the effects of light and moisture on survivor vigor. Extrapolation of the effects such as fire intensity (as manipulated via the burn piles) to areas outside research plots should be approached with caution.

Trail and South Areas have not experienced fire since 1965 and 1966 respectively (with the exception of a nearby management burn that burnt into the corner of South Area near Subarea 7). The buildup of fuel in the two areas (Table 5) reflects a long inter-fire interval, an interval that far exceeds the 2-10 yr "natural" fire interval suggested by Kilgore and Taylor (1979), Swetnam (1993) and Swetnam et al. (1992) for low to moderate intensity fires or the 10-35 yr interval suggested by Kilgore and (Talyor 1979) for low intensity fires with patchy high intensity. There was such a heavy fuel load of downed logs and dead snags in Trail and South Areas in the mid -1960's that we created burn piles to avoid creating conditions hot enough to heavily scorch large trees or start crown fires. Because we used burn piles in this manner we created relatively low intensity surface burns in the other parts of the study areas, which in turn did not heat kill many of the intermediate-sized white firs as has been the case in prescribed fires carried out in Sequoia and Kings Canyon National Parks since the time of our study; the Park prescribed fires typically have been hotter than ours were and have better reduced the stands density of white firs (Abies concolor) as well as total fuel loads (Keifer 1998). Our fires were hot enough to create a heavy seed fall and to remove surface litter and vegetation, and hence allow for germination, but not hot enough to open up the canopy. Our "hot spots" therefore were much smaller than those described by Kilgore and Taylor (1979), and discussed further by Stephenson (1994), for low intensity fires with patches of higher intensity.

As of the year 2000, both South and Trail Areas were approaching a "ladder type" forest structure as it pertains to fire, with abundant downed wood, a thick layer (or subcanopy) of shrubs and small trees and an intermediate subcanopy of white firs and incense cedars that have the potential to carry future fires into the lower branches and hence into the crowns of the mature trees in these areas. Two, or likely more, fire intervals under natural conditions (Kilgore and

Taylor 1997; Swetnam 1993; Swetnam et al. 1992) have passed since the inception of this study. The amount of surface and subcanopy vegetation that has built up from what was essentially bare and burned mineral soil in 1965 and 1966 provides all those who observe these areas with a graphic reminder of not only the role of fire in the regeneration of giant sequoia groves but also the problems that arise when frequent fires are excluded from them. Our study, and those of others (Kilgore and Taylor 1997; Swetnam 1993; Swetnam et al. 1992), indicate that controlled burns need to be applied to the groves on a regular basis to set back succession, promote continued regeneration of giant sequoias and protect the groves from destructive crown fires.

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